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A CLIMATIC DRIVER FOR ABRUPT MID-HOLOCENE VEGETATION DYNAMICS AND THE HEMLOCK DECLINE IN NEW ENGLAND

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Abstract. The mid-Holocene decline of eastern hemlock is widely viewed as the sole prehistorical example of an insect- or pathogen-mediated collapse of a North American tree species and has been extensively studied for insights into pest–host dynamics and the consequences to terrestrial and aquatic ecosystems of dominant-species removal. We report paleoecological evidence implicating climate as a major driver of this episode. Data drawn from sites across a gradient in hemlock abundance from dominant to absent demonstrate: a synchronous, dramatic decline in a contrasting taxon (oak); changes in lake sediments and aquatic taxa indicating low water levels; and one or more intervals of intense drought at regional to continental scales. These results, which accord well with emerging climate reconstructions, challenge the interpretation of a biotically driven hemlock decline and highlight the potential for climate change to generate major, abrupt dynamics in forest ecosystems.

Key words: *climate change; forest dynamics; hemlock decline; Holocene; New England (USA); oak decline; paleoecology; pollen record.*

INTRODUCTION

Understanding the dynamics and controls of broad-scale outbreaks of pests and pathogens in forest ecosystems is of fundamental and practical importance due to their profound impacts on ecosystem structure and function, and consequences for biodiversity and regional economies (e.g., Anderson et al. 2004). One extensively studied paleoecological benchmark for such biotic impacts is the abrupt decline of eastern hemlock (*Tsuga canadensis*) ~5500 years ago, which is portrayed as the sole example of a prehistorical pest or pathogen outbreak in North America, and one of the most important examples of temperate forest dynamics since deglaciation (Webb 1982, Allison et al. 1986, Foster and Zebryk 1993, Fuller 1998, Bennett and Fuller 2002). Historically interpreted as driven by climate change (Deevey 1939), the hemlock decline was first attributed to a pest or pathogen by M. B. Davis (1981). Davis' and subsequent interpretations (e.g., Allison et al. 1986, Davis 1989) are based on the observation that the decline appeared to be (a) species specific, (b) range wide (Webb 1982, Bennett and Fuller 2002), (c) synchronous (currently dated at 4750 ¹⁴C yr = 5500 calendar years

before present) (Bennett and Fuller 2002), and (d) abrupt, with a palynological signature analogous to the historical chestnut blight (*Cryphonectria parasitica*), which eliminated American chestnut (*Castanea dentata*) as an overstory tree in eastern North America (Allison et al. 1986). The suggestion by Davis (1981) that an insect like the eastern hemlock looper (*Lambdina fiscellaria*) may have been responsible for this dynamic gained support when fossil remains of the looper and chewed hemlock needles were located in sediments exhibiting a pollen record of the decline (Anderson et al. 1986, Bhiry and Filion 1996). Alternatively, many entomologists suggest that the signature and duration of the hemlock decline is inconsistent with that of known insect impacts and more analogous to a fungal or viral pathogen (J. Elkinton, *personal communication*). This pathogenic interpretation has also been favored by other paleoecological studies (Allison et al. 1986, Davis 1989).

Over the years numerous researchers examining long-term vegetation and climate dynamics have questioned Davis' interpretation that biotic factors were the major driver of the hemlock decline and have suggested that the proximal factor may be broad-scale climatic change. Recently, considerable paleoclimatic evidence has emerged indicating that the decline coincided with a dry climatic interval that induced regional-to-continental changes in vegetation and water levels (Yu and

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TABLE 1. Sites in southern New England, USA, mentioned in the text.

Site	N latitude (°)	W longitude (°)	Elevation (m)	Reference
Study sites				
Berry Pond East	42.620	-71.087	43	Oswald et al. (<i>in press</i>)
Berry Pond West	42.505	-73.319	631	Whitehead (1979)
Black Gum Swamp	42.536	-72.214	358	Foster and Zebryk (1993)
Blaney's Pond	41.467	-70.767	15	W. W. Oswald and D. R. Foster (<i>unpublished data</i>)
Blood Pond	42.080	-71.962	214	Oswald et al. (<i>in press</i>)
Cedar Tree Neck Bog	41.428	-70.700	20	Stevens (1996)
Deep Pond	41.581	-71.640	23	W. W. Oswald and D. R. Foster (<i>unpublished data</i>)
Duck Pond	41.933	-70.001	3	Winkler (1985)
Fresh Pond	41.161	-71.579	28	Dunwiddie (1990)
Hawley Bog	42.575	-72.890	549	W. A. Patterson (<i>unpublished data</i>)
Little Pond	42.675	-72.192	302	Oswald et al. (<i>in press</i>)
Mohawk Pond	41.817	-73.283	360	Gaudreau (1986)
No Bottom Pond	41.285	-70.114	8	Dunwiddie (1990)
North Pond	42.651	-73.054	586	Whitehead and Crisman (1978)
Rogers Lake	41.367	-72.117	91	Davis (1969)
Wildwood Lake	40.892	-72.673	5	W. W. Oswald and D. R. Foster (<i>unpublished data</i>)
Winneconnet Pond	41.971	-71.133	22	Suter (1985)
Other sites				
Crooked Pond	41.892	-70.650	28	Shuman et al. (2001)
Makepeace Cedar Swamp	41.933	-70.766	40	Newby et al. (2000)
Owl Pond	41.770	-70.016	7	Tzedakis (1992)

McAndrews 1994, Yu et al. 1997, Haas and McAndrews 2000, Shuman et al. 2001, 2004, 2005b, Calcote 2003). These findings, coupled with evidence that mid-Holocene climate fluctuations may be linked to changes in solar activity (Magny and Haas 2004, Magny et al. 2006), raise again the potential of an important role for environmental change in this striking forest dynamic.

Identification of the factors controlling the hemlock decline and recovery has importance because many studies have drawn far-reaching ecological and evolutionary interpretations based on the assumption that the decline is a model system for the reduction of a single species independent of environmental drivers (Fuller 1998, Foster 2000). These interpretations bear on such fundamental processes as: (a) forest succession and ecological resilience (Fuller 1998, St. Jacques et al. 2000), (b) terrestrial-aquatic ecosystem coupling and the relationship between ecosystem nutrient retention and biomass dynamics (Hall and Smol 1993, St. Jacques et al. 2000), (c) synergies between natural disturbances (e.g., pest outbreaks and fire) (Foster and Zebryk 1993), (d) equilibrium of the vegetation-climate system (Fuller 1998, Shuman et al. 2004), and (e) the evolutionary biology of pest-host systems (Davis 1981, 1989).

METHODS

To interpret the mid-Holocene environmental and ecological dynamics surrounding the hemlock decline, we investigated changes in forest composition and sediment characteristics between 8000 and 2000 calendar years before present at 17 sites across southern New England (USA) and compared these to regional and global climatic reconstructions (Table 1, Fig. 1). The sites span a biophysical gradient from the higher-elevation inland region of Massachusetts, with cool,

moist climate and a relatively short growing season, to lower-elevation coastal areas of New York, Rhode Island, and Massachusetts, which are characterized by warmer, drier climate and a three-week-longer growing season (Foster and Aber 2004). Modern vegetation ranges from northern hardwood-hemlock-white pine (*Pinus strobus*) forest on shallow till soils inland to a complex of vegetation on deep glacial deposits in the coastal region of Cape Cod and adjacent islands (Foster and Aber 2004). Near the coast, finer-textured soils support oak (*Quercus* spp.) with some beech (*Fagus grandifolia*) and maple (*Acer* spp.), whereas pitch pine (*Pinus rigida*) and scrub oak (*Quercus ilicifolia*) predominate on coarse-grained outwash soils. This regional environmental gradient also appears to have controlled patterns of vegetation during the Early Holocene, when hemlock was abundant in the northwestern portion of the study area but rare or absent along the coast (Fig. 1).

Pollen and chronological data were obtained from the North American Pollen Database (*available online*)⁴ and Harvard Forest studies. Radiocarbon dates were converted to calendar years before present (cal. yr BP) using OxCal 3.9 (Bronk Ramsey 2001) and age-depth models were constructed by linear interpolation between selected dates. We examined the timing, rate, magnitude, and compositional direction of vegetation changes across this relatively small region (500 × 200 km), and compared these dynamics with local, regional, and global records of past environmental variability. By examining changes across the regional gradient, we sought to disentangle the relative impact of hemlock dynamics vs. environmental changes on overall forest dynamics.

⁴ www.ncdc.noaa.gov/paleo/napd.html

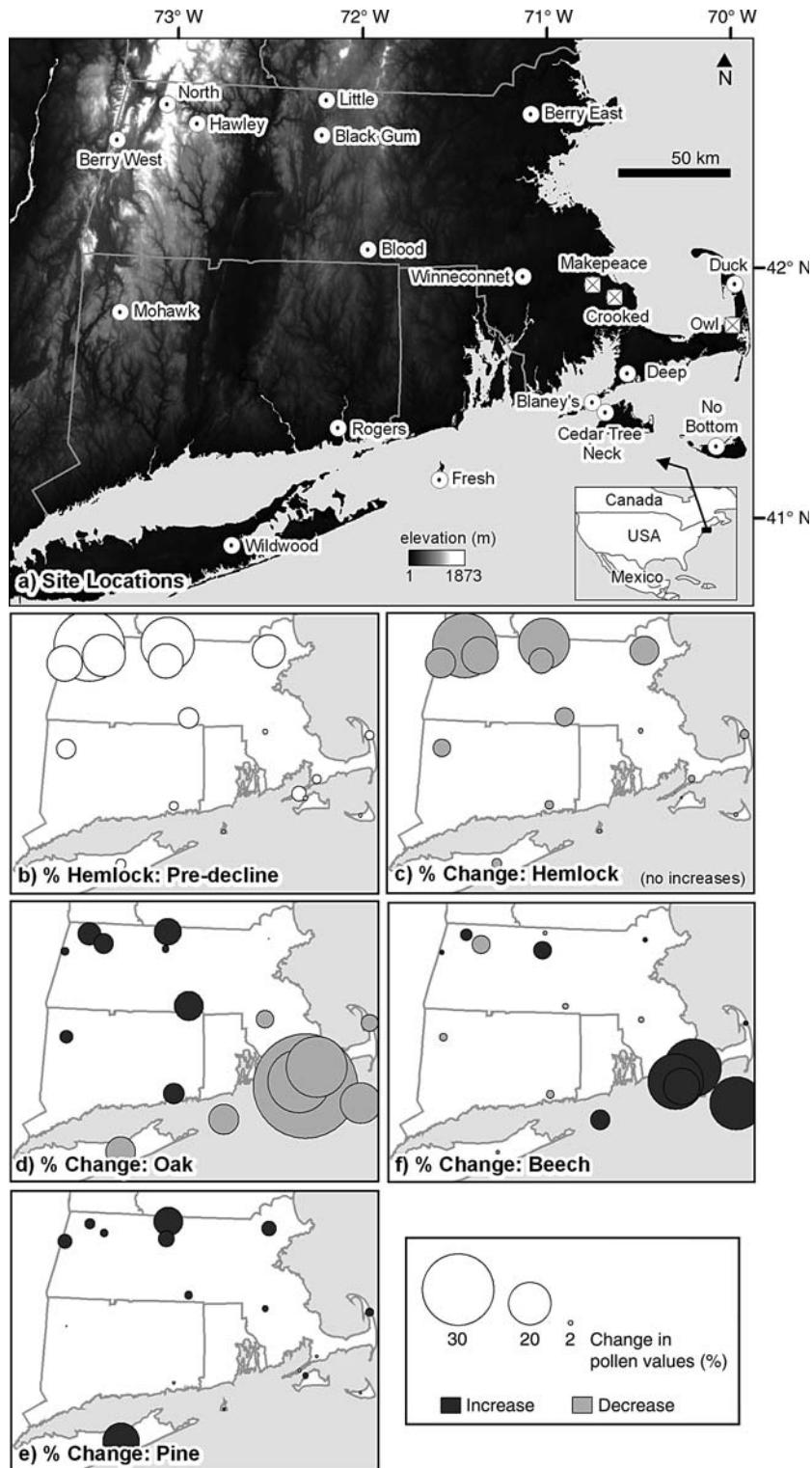


FIG. 1. (a) Map of study sites (circles) and other cited locations (squares; Tzedakis 1992, Newby et al. 2000, Shuman et al. 2001) in southern New England, USA. (b) Percentage pollen values for hemlock for samples immediately before the hemlock decline. Hemlock pollen abundance varied from >30% at inland sites to 0–5% on the coast. (c–f) Change in pollen percentage values for various taxa during the hemlock decline, calculated as the difference between the sample immediately before the decline (average age \pm SD = 5490 \pm 190 yr) and the sample where hemlock abundance is lowest (4260 \pm 510 yr). Regression of pre-decline hemlock percentage vs. the percentage change at the decline yields $r^2 = 0.99$.

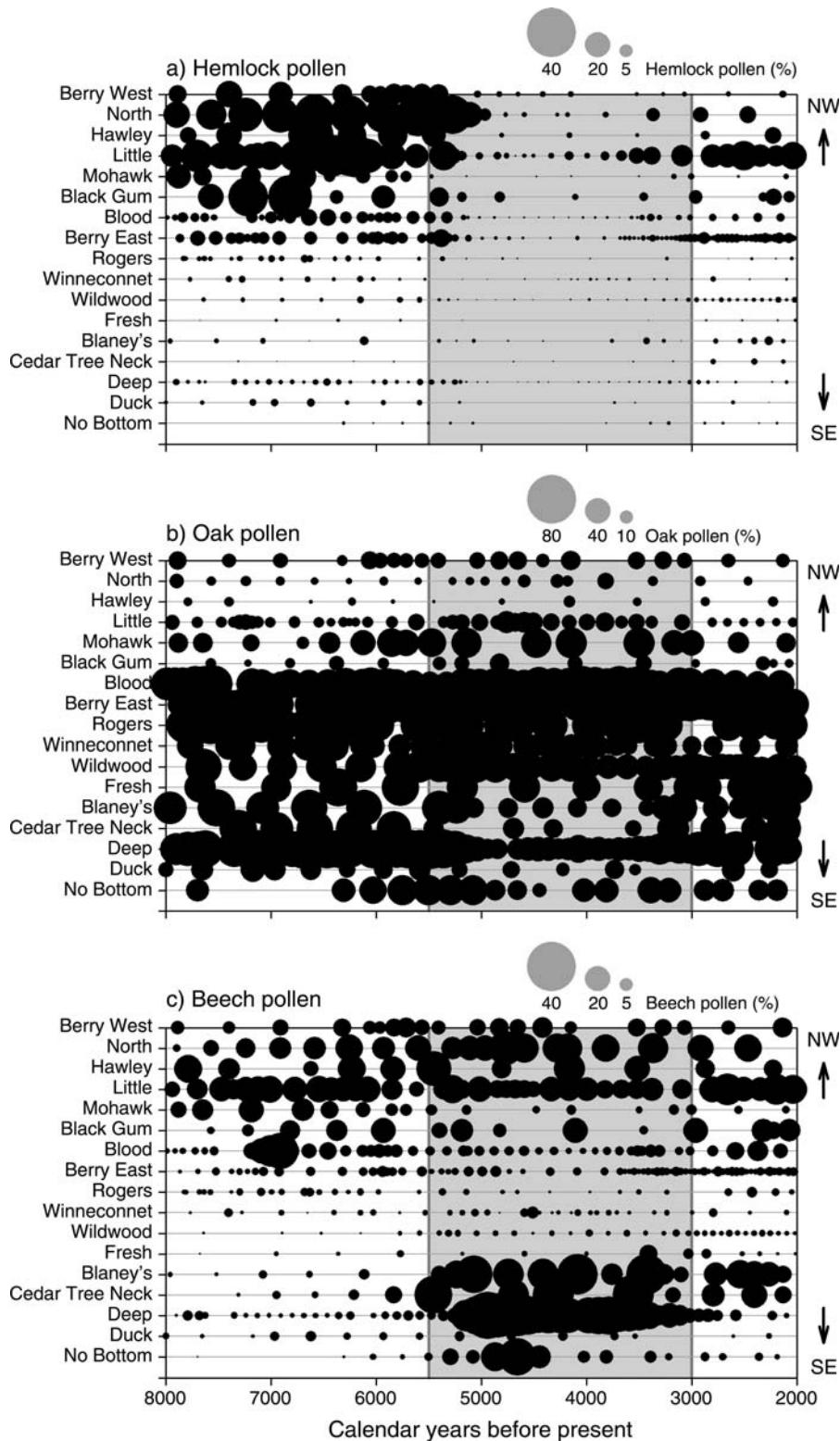


FIG. 2. Pollen data from 17 study sites in southern New England (for site locations see Fig. 1): (a) hemlock pollen percentage values, illustrating the mid-Holocene interval of low hemlock abundance in the northwestern portion of the study area; (b) oak pollen percentage values, showing the mid-Holocene decline of oak at several coastal sites; and (c) beech pollen percentage values, with elevated abundance at several coastal sites during the mid-Holocene interval. Shading delineates the interval of dry climate between 5500 and 3000 cal. yr BP.

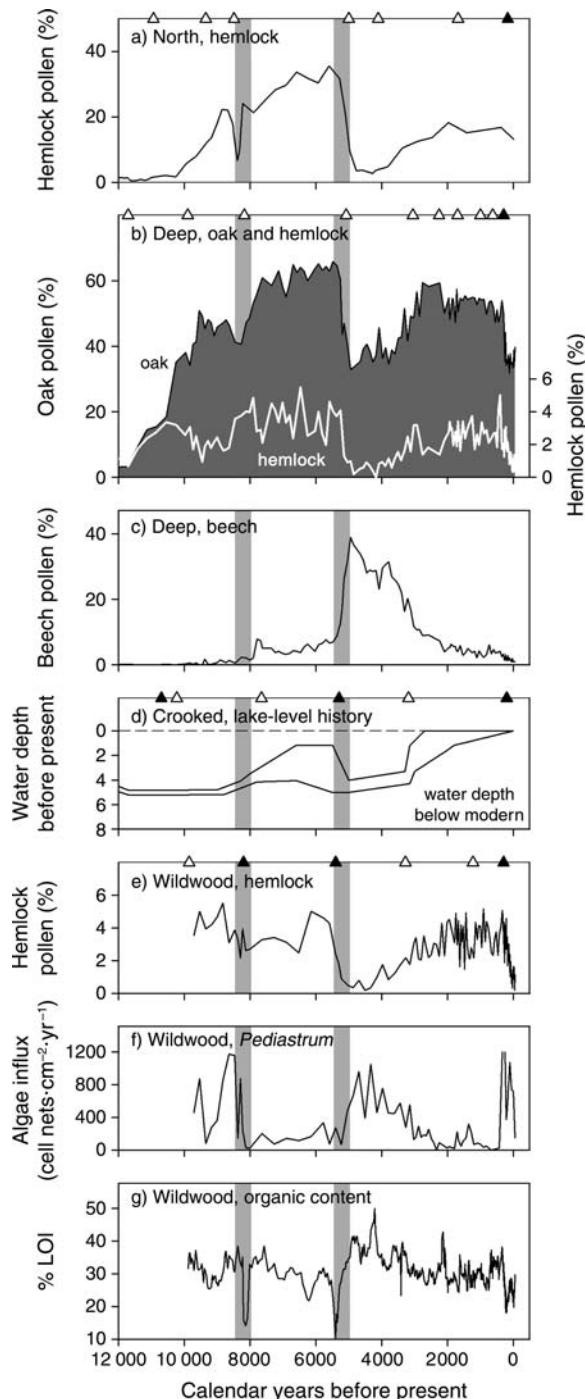


FIG. 3. Paleoecological data from key sites across southern New England (Fig. 1) for 12 000 cal. yr BP to the present. (a) Hemlock pollen percentage for North Pond, exhibiting low values at ca. 8200 cal. yr BP and during the mid-Holocene interval. (b) Oak and hemlock pollen percentage for Deep Pond; note the similarity between the stratigraphic patterns of oak at Deep Pond and hemlock at North Pond. (c) Beech pollen percentage for Deep Pond, featuring the interval of high abundance between ca. 5500 and 3000 cal. yr BP. (d) Reconstruction of past variations in water depth (meters below modern) for Crooked Pond (Shuman et al. 2001); note the interval of low lake level coincident with the mid-Holocene

RESULTS

The period 5500–3000 cal. yr BP is characterized by geographically consistent changes in vegetation across southern New England, USA (Figs. 1 and 2). The hemlock decline is (a) abrupt at all sites, (b) proportional to its pre-decline abundance, and (c) apparently synchronous and chronologically consistent with other studies (Bennett and Fuller 2002). At inland sites, where the hemlock decline is most striking, there are corresponding increases in the abundance of oak and pine (*Pinus* spp.). Pollen-influx data (not shown) show a similar pattern, with increased values for several taxa during the interval of reduced hemlock abundance. However, many coastal sites, where hemlock was rare, display a strikingly different dynamic. Oak, the dominant coastal taxon prior to 6000 cal. yr BP, declines by as much as 50% (Figs. 1 and 3), while beech, which changes slightly and variably at inland sites, increases 10–25% to reach its highest Holocene values ca. 5000 cal. yr BP. This pattern is most pronounced at sites on southwestern Cape Cod and the adjacent islands. A somewhat different change takes place at Owl Pond (Tzedakis 1992) and Wildwood Lake, Long Island, New York, where the decline in oak is associated with a minor change in beech and a major rise in pitch pine. Although hemlock pollen percentages are low at all coastal sites (Fig. 1) their abrupt decline at ca. 5500 cal. yr BP provides stratigraphic confirmation that the inland-hemlock and coastal-oak declines are exactly contemporaneous (Fig. 3). Hemlock values remain low at inland sites until ca. 4000 cal. yr BP, at which point they increase gradually until ca. 3000 cal. yr BP (Figs. 2 and 3). Similarly, at coastal sites a parallel increase in oak pollen percentages commences ca. 4000 cal. yr BP and continues through ca. 3000 cal. yr BP. Beech declines to a lower regional abundance by ca. 3000 cal. yr BP.

DISCUSSION

This paleoecological evidence casts strong doubts on the interpretation of the hemlock decline in southern New England (USA) as caused solely by a pest or pathogen. The compositional changes at inland and coastal sites involved tree taxa that differ greatly in

hemlock and oak declines. Regression of North hemlock vs. Deep oak pollen percentage (average values for 400-year intervals between 8600 and 1800 cal. yr BP) yields $r^2 = 0.74$. (e) Hemlock pollen percentage for Wildwood Lake; values are relatively low overall, but the mid-Holocene decline is evident. (f) *Pediastrum* algae influx values for Wildwood; the high mid-Holocene values indicate a change in lake level and/or nutrient status during that interval. (g) Organic content (percentage loss-on-ignition, % LOI) for Wildwood, featuring abrupt declines at ca. 8200 and 5500 cal. yr BP. Vertical shading highlights changes in various proxies at ca. 8200 and ca. 5500 cal. yr BP. Triangles show data points used in the age–depth model for each site: open triangles are ^{14}C dates; solid triangles are age assignments based on pollen stratigraphy.

physiology, morphology, pathology, ecology, and broad-scale distribution (Thompson et al. 1999), and yet the observed changes in these taxa were synchronous and equivalent in magnitude and rate (Fig. 3). We suggest that mid-Holocene climate change, rather than a biological agent, was the primary driver of both the hemlock decline in the inland region and the decline of oak and increase of beech at coastal sites. This finding adds considerable support to earlier suggestions regarding a link between climate and the hemlock decline (e.g., Yu and McAndrews 1994, Haas and McAndrews 2001, Calcote 2003, Shuman et al. 2004), but it does not exclude the possibility that pests or pathogens may have affected hemlock trees in response to their stressed condition or the altered climate setting (cf. Bhiry and Fillion 1996, Haas and McAndrews 2001, Shuman et al. 2001, Calcote 2003).

*Regional evidence for dry climate
during the middle Holocene*

Diverse paleoenvironmental evidence indicates that substantial mid-Holocene climate changes occurred in New England, elsewhere in northeastern North America, and possibly at the global scale. For example, water-level reconstructions in southeastern Massachusetts indicate that the interval of the hemlock and oak declines was characterized by extremely low moisture availability (Shuman et al. 2001). At Crooked Pond, lake levels dropped 2–3 m (~4 m below present-day level) at ca. 5500 cal. yr BP and remained low until ca. 3000 cal. yr BP (Fig. 3), whereas sediments at Makepeace Cedar Swamp shifted from lacustrine mud to peat at ca. 5300 cal. yr BP (Newby et al. 2000). Likewise, increased abundance of *Pediastrum* algae from ca. 5000 to 3000 cal. yr BP in sediments from Wildwood Lake on Long Island (Fig. 3) suggests a region-wide change in water levels, perhaps accompanied by changes in nutrient status (e.g., Jankovska and Komarek 2000, Komarek and Jankovska 2001). Lake-level studies from other sites in northeastern North America reveal similar mid-Holocene changes (e.g., Lavoie and Richard 2000, Dieffenbacher-Krall and Nurse 2005, Shuman et al. 2005b). Meanwhile, analyses of sediment isotope geochemistry suggest that these dry conditions between ca. 6000 and 3000 cal. yr BP resulted from changes in large-scale atmospheric circulation patterns (Yu et al. 1997, Kirby et al. 2002).

In addition to hemlock and oak, other taxa also exhibit changes indicative of warm, dry conditions during the middle Holocene. For example, hickory (*Carya*), a tree that prefers relatively warm conditions and reaches its present-day northern range limit in southern New England, increases at sites across the region at ca. 6000 cal. yr BP (e.g., Shuman et al. 2004). The pollen record from Hemlock Hollow, located near the Black Gum Swamp at the Harvard Forest in central Massachusetts (Fig. 1), features a decline in birch (*Betula*) between ca. 6000 and 3300 cal. yr BP, also

indicating warm, dry climatic conditions (Foster and Zebryk 1993). This site also exhibits vegetational evidence for an increase in effective moisture coinciding with the post-decline increases in oak and hemlock at ca. 3300 cal. yr BP. The Hemlock Hollow record shows that spruce (*Picea*), a northern or montane taxon that occupies wetlands in southern New England, increased in abundance at that time. A coincident shift to cooler conditions is also indicated by a decrease in the maximum elevation of white pine and hemlock in the Adirondacks (New York) and White Mountains (New Hampshire) (Davis et al. 1980, Jackson and Whitehead 1991, Spear et al. 1994).

*Evidence for an abrupt climatic event
at ca. 5500 cal. yr BP*

The long duration (~3000 years) and large spatial extent of the mid-Holocene changes in forest composition in northeastern North America are consistent with orbital-scale variations in synoptic climatology (e.g., Shuman et al. 2005a). On the other hand, the abrupt onset of the hemlock and oak declines is somewhat enigmatic given our current understanding of Holocene climate history. Emerging evidence from high-resolution analyses of lake sediments from southern New England and elsewhere, however, suggests that these abrupt changes coincided with one or more intervals of intense drought. For example, at Wildwood Lake the drop in hemlock pollen percentages is coincident with a brief, but dramatic, decline in organic content (Fig. 3). Similarly, strong, century-scale droughts appear at 5800 and 5300 cal. yr BP at Shephard Lake, Ontario (Haas and McAndrews 2000), and the ostracode record from Elk Lake, Minnesota, USA, indicates prolonged low-water events at 5400 and 5200 cal. yr BP (Smith et al. 2002). In fact, major climatic shifts between 6000 and 5000 cal. yr BP, ascribed to changes in solar activity and/or oceanic circulation, have been observed in paleoenvironmental records from sites worldwide (Magny and Haas 2004, Magny et al. 2006). A decline in hemlock in response to sharply reduced moisture availability is consistent with its environmental tolerances, as hemlock has high moisture requirements relative to other common New England trees (Thompson et al. 1999, Shuman et al. 2004).

Long-term parallels in coastal oak and inland hemlock

Early-Holocene vegetation changes at sites in southern New England provide additional insights into the mid-Holocene environmental and ecological dynamics, as they demonstrate the striking similarities between the long-term records for coastal oak and inland hemlock (Fig. 3), confirming that these changes parallel regional and global climate. From ca. 10 000 cal. yr BP onwards, oak pollen percentages at Deep Pond closely match those for hemlock at North Pond in overall trajectory and specific details. These details include an abrupt decline at ca. 8200 cal. yr BP, which various lines of

evidence (Shuman et al. 2002, 2004, Alley and Ágústsdóttir 2005), including a drop in organic content in Wildwood Lake sediments (Fig. 3), identify as a brief, dramatic interval of cold and dry conditions. The similarity between variations in inland hemlock and coastal oak abundance throughout the Holocene and the clear relationship between those variations and both gradual, long-term and rapid, short-term climate changes present a compelling argument that the mid-Holocene decline in both species was driven by climate.

Reevaluation of the relevance of the hemlock decline

The close association between climate change and vegetation dynamics highlighted here strengthens the assertion of Webb (1986) and Shuman and colleagues (2004) that at many spatial scales forest dynamics are in equilibrium with regional climate. Notably, and contrary to many previous assertions, the mid-Holocene hemlock decline does not provide an example of ecological disequilibrium and should not be used as a model system for investigating ecological and evolutionary processes surrounding the selective removal of a single species (Davis 1981, Fuller 1998). Similarly, interpreted changes in lake productivity, water levels, and sediment characteristics coincident with the decline are likely more strongly tied to the direct effects of changes in temperature, precipitation, moisture balance, and hydrology than to the indirect consequences of forest-ecosystem dynamics and associated changes in evapotranspiration, biomass accumulation, and nutrient retention (Hall and Smol 1993, St. Jacques et al. 2000). Finally, if the hemlock decline was strongly driven by climate, it does not offer insights into recent and ongoing pest and pathogen outbreaks like the chestnut blight and the hemlock woolly adelgid, as has been asserted (Allison et al. 1986, Foster 2000).

Nonetheless, this climate-centric interpretation of mid-Holocene vegetation dynamics has great relevance to present-day ecological issues and understanding. First, this finding supports the contention that climate change may generate quite rapid and pronounced changes in regional forest composition (e.g., Ammann et al. 2000, Tinner and Lotter 2001, Williams et al. 2002). Although our stratigraphies are not tightly constrained chronologically, we record massive declines in hemlock and oak occurring over less than ~500 years. These results also present an opportunity to explore the range of adjustments in ecological, biophysical, and cultural systems under a major regional change in environment and vegetation. Consequently, this episode offers some interesting insights into systems like those in the modern world that are exposed to rapid environmental change. From this perspective our results underscore the extreme difficulty in sorting out the complex interactions among the environmental and biological systems that drive broad ecosystem dynamics, even in the absence of the additional complications interjected by substantial human activity.

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